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High and dry or sunk and dunked: lessons for tallgrass prairies from quaking bogs

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Abstract Northern Wisconsin bogs provide a natural experiment on butterfly population occurrence in a naturally highly fragmented vegetation type, which may provide insight on conserving butterflies in anthropogenically fragmented and degraded landscapes. We surveyed butterflies in bogs (about as unaffected by humans as possible, but naturally occurring over <1% of northern Wisconsin) primarily during 2002–2009, with additional observations from 1986 to 2001. Different bog types had different bog-specialist butterfly faunas, but bog butterfly abundance also differed in similar vegetations among subregions. Some small isolated bogs held very high densities of specialist butterflies. Summer but not spring specialists frequented adjacent lowland roadsides and utilized a variety of non-native as well as native nectar sources. Paleo-entomology indicates that insects don't evolve out of trouble; instead they move out of trouble. Given the low dispersal apparent today for species restricted to bogs, "move" might be better understood as "hunkering" within their vegetation as it expands and shrinks and moves around the landscape. Although bogs appeared to have more intact specialist butterfly faunas than tallgrass prairies (99.9% destroyed by human activities), bog butterflies do not live in average sites even in a relatively natural landscape. Just as bog butterflies are "sunk and dunked" in isolation, specialist butterflies elsewhere may have been left "high and dry" naturally, or are now due to human activities. Numerous studies have demonstrated that presence and abundance of specialist butterflies increase with increasing size and connectedness of habitat patches. But with long-term consistent vegetation, populations with high abundances in small isolated sites and with low numbers thinly occurring in large sites can be secure, as shown by bog butterflies.

Keywords Bog · Specialist butterfly · Population persistence · Dispersal · Co-evolution · Stasis · Habitat quality · Landscape configuration · Habitat fragmentation · Vegetative consistency

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Introduction

A major threat to biodiversity is human-caused habitat loss and fragmentation, with degradation of extant patches by edge effects and disruption of ecological processes (Brown 1997; van Swaay et al. 2006; Forister et al. 2010). Butterfly populations fare more poorly in isolated or small sites, with nearer and larger sites more likely to remain occupied or become re-colonized (Bulman et al. 2007; Hanski and Pöyry 2007; Dover and Settele 2009). Both habitat quality and landscape configuration are important for maintaining butterfly populations (Dennis and Eales 1997; Thomas et al. 2001; Hanski and Pöyry 2007; Dennis 2010), and both are under more threat in a human-degraded, fragmented landscape. As a result, much research in conservation biology concerns how to counteract the effects of habitat loss, degradation, and fragmentation on vulnerable species (e.g., Mattoni et al. 2001; Thomas et al. 2001; Dennis and Hardy 2007; Swengel and Swengel 2007; Spencer and Collins 2008; Dennis 2010).

In the midwestern USA, tallgrass prairie (predominately herbaceous flora) and oak savanna (trees and brush mixed in with herbaceous patches) have been about 99% destroyed primarily by conversion to agriculture (Curtis 1959; Nuzzo 1986; Samson and Knopf 1994). Pine barrens (a savanna on very sandy soil) have also declined but not to

the same degree (Curtis 1959; Riegler 1995). Fragmentation and degradation greatly affect remaining examples of these vegetations and their associated butterflies (Samson and Knopf 1994; Riegler 1995; Swengel and Swengel 1999a, 2001).

In temperate areas of North America and Europe, bog (peatland) vegetation is also rare, being naturally isolated and forming a low proportion of the natural landscape. Although often viewed as a long-lived successional stage between open water and forest in glaciated landscapes, peatlands can get reset to an earlier successional stage (Curtis 1959). Since bogs are well known for their relatively stable vegetations and insect faunas over the long term, they can also be viewed as a climax community (Spitzer et al. 1999; Spitzer and Danks 2006; Whitehouse 2006; Whitehouse et al. 2008). While often considered relatively uniform floristically both within and among sites, bogs actually contain many microhabitats (Väisänen 1992; Spitzer and Danks 2006; Turlure et al. 2009, 2010). In Wisconsin, bogs occur primarily in central and northern areas (Curtis 1959). Prior to European settlement, peatlands occurred in <1% of the Wisconsin landscape (even counting only the northern third of the state), and most of that vegetation is still extant, with only 9% loss (Hoffman 2002), more lost in central than northern Wisconsin. Much of what is left, especially in northern Wisconsin, is relatively undegraded. Primary human impacts are roads and ditches; adjacent lands are more affected by timber harvesting, agriculture, and urbanization (pers. obs.). Conversion to cranberry agriculture and peat harvesting has occurred more in central Wisconsin bogs (Curtis 1959). By contrast, in Europe bog vegetation is much destroyed and degraded by human activities, along with the associated butterfly species of high conservation concern (Vandewoestijne and Baguette 2004; Schtickzelle et al. 2006; Spencer and Collins 2008; Turlure et al. 2009). The four bog-related vegetation types ranked highest in proportion of threatened butterfly species of their typical faunas (van Swaay et al. 2006).

In addition to observations by a few other lepidopterists, Nekola (1998) conducted a systematic survey of northern Wisconsin peatlands and their associated butterflies in 1996. He described three peatland types: muskeg (black spruce-cottongrass-wiregrass savanna similar in elevation to surrounding uplands), kettlehole (sphagnum-leatherleaf mats, often floating on lakes or sunk in depressions much lower than the surrounding landscape), and coastal peatland (tamarack-sedge mats with ridges of muskeg-like vegetation in estuaries along the Lake Superior coast). Many aspects of the flora are similar among these three types (Nekola and Kraft 2002), echoing Curtis's (1959) description of remarkably uniform bog structure and composition throughout the circumboreal region. Nekola (1998) nevertheless found significant differences in bog-obligate butterfly occurrence among these three bog types, and noted variation in flora amongst sites, especially kettleholes.

We have recorded butterflies in Wisconsin bogs since 1986. In this paper, we analyze these results to expand and extend Nekola's study in order to describe patterns of bog butterfly occurrence and abundance. We examine butterfly occurrence and abundance in bogs in relation to bog type, size, and isolation, and in adjacent lowland roadside ditches and nearby upland roadsides. This provides evidence on the relative importance to specialist butterfly population persistence of dispersal tendency, habitat quality, and landscape configuration. During the same period, we conducted surveys of butterflies in prairies in seven midwestern states (Swengel 1996; Swengel and Swengel 1999b, Swengel and Swengel 2007) and Wisconsin pine barrens (Swengel 1998; Swengel and Swengel 2005, 2007). Based on this field work and others' studies, we contrast the occurrence of specialist butterflies between vegetations altered and fragmented by humans (prairie, barrens) and naturally fragmented ones (bogs). These results should be useful for application to conservation of bog butterflies where they are vulnerable, and vulnerable butterflies in other fragmented vegetations.

Methods

Study regions

The primary study region contains 73 bog sites scattered across an area 367 km east–west by 169 km north–south (45.33–46.86°N, 88.21–92.56°W) in twelve contiguous counties spanning the entire breadth of northern Wisconsin. At 20 of these sites, we also surveyed the lowland (wetland) roadside ditch through or adjacent to the bog, and at five sites, we surveyed a more upland roadside corridor 20–350 m from the bog. In three large muskeg complexes, we counted surveys in each separate area as a separate site. In central Wisconsin, the three bogs in two contiguous counties (Jackson, Wood) are in an area 29 km east–west by 4 km north–south (44.31–44.34°N, 90.19–90.56°W), which is 169 km south of the nearest study site in the northern study region. Nekola's (1998) study region comprises sites in and adjacent to the Lake Superior drainage basin in four contiguous counties (Ashland, Bayfield, Douglas, Iron) bordering the south lakeshore. This area is the north part of the west half of our northern study region. All our sites in those counties fall within his study region.

Within each study region, we biased toward high-quality examples of bog vegetation that were open to public visitation and efficient to gain access to and travel between due

to clustering of sites and/or efficient routing among sites, including proximity to other kinds of sites of interest for other species. Nonetheless, peatlands often present difficulties of access both to them and across them, which reduces efficiency and amount of transect distance surveyed in a day. Roadside survey areas were selected because we noticed bog butterflies using them, they were en route to or from a bog survey route, or they appeared potentially of interest for either bog or other butterfly species.

Surveys

On 114 informal visits during 1986–2001 in both study regions (widely in the northern one), we recorded number of individuals by species per site, but did not standardize a route or record weather and effort (time and distance spent surveying). We began formal transect surveys in bogs in 1990, with most conducted during 2002–2009 (Table 1). In those last 8 years, we surveyed in a rotation through the western, central, and eastern sections of the northern study region, trying to cover one section per weekend, or more if a section was missed the previous weekend and/or if time allowed. But we missed an occasional weekend per year due to weather or another commitment. Surveys occurred between 23 April and 12 September, usually early/mid May through early/mid August in most years. We also continued to record bog specialists informally observed in uplands and roadsides as we accessed bogs for formal surveys.

Our peatland transect surveys were like those in prairie and barrens (similar to Pollard 1977 and as described in Swengel 1996, 1998; Swengel and Swengel 1997). We walked along a similar route per visit to a prairie, barrens, or bog at a slow pace (about 2 km/h) on parallel routes 5-10 m apart. We counted all adult butterflies observed ahead and to the sides, to the limit at which an individual could be identified, possibly with the aid of binoculars after detection, and tracked. A new sampling unit was designated whenever the vegetation along the route varied by management (type and/or years since last treatment), type (wet, mesic, dry), quality based on type of brush and diversity and abundance of native and exotic flora (undegraded, semi-degraded, highly degraded), and/or estimated macrosite canopy (grassland or open bog < 10%, open savanna 10-24%, closed savanna 25-49%, forest opening 50-75%). Routes crossed rather than followed ecotones and management boundaries to reduce edge effects, and were designed to minimize number of unit changes while covering representative areas of the site. Temperature (starting, ending, low, high), wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying were recorded for each unit. Data from each unit were kept separate. Surveys occurred during a wide range of times of day and weather, occasionally in intermittent light drizzle so long as butterfly activity was apparent, but not in continuous rain. All butterfly species found were counted, but survey times and locations were selected to study butterflies specialized to that vegetation.

Table 1 *N* surveys of units and survey effort (km, h) in central and northern Wisconsin at 76 bog sites, 20 lowland roadsides, and 5 upland roadsides, from 23 April to 12 September

	N	Years	Km	Hours
1987–2001				
All sites	50	1987–2001	44.0	25.8
Bog	27	1990–2001	21.5	13.1
Lowland	5	1999–2001	3.1	2.1
Upland	18	1987–1996, 1998–2001	19.5	10.7
2002–2009				
All sites	1,973	2002–2009	921.9	377.2
Bog	1,699	2002–2009	806.5	321.3
Lowland	223	2002–2009	80.5	42.5
Upland	51	2002–2009	34.9	13.5

In prairie and barrens, we categorized the species by habitat niche breadth (Swengel 1996, 1998): (1) specialist (restricted or nearly so to herbaceous flora in prairie and/or savanna; sensitive to vegetative quality); (2) grassland species (widely inhabiting both native and degraded herbaceous flora); (3) generalist (inhabiting grassland and other vegetation types); and (4) immigrant (occurring in the study region during the growing season but unlikely to overwinter). In bogs, we used an analogous categorization applicable to this study region only, and these categories correspond approximately to those (in parentheses) described by Spitzer and Danks (2006) (Table 2): (1) bog specialist (tyrphobiontic)—restricted or nearly so to peatlands; (2) bog affiliate (tyrphophilic)—breeding in bogs as well as other vegetations (limited to species of north temperate or boreal affinity); (3) generalist (tyrphoneutral)—year-round resident primarily using vegetation other than bogs (if the species also breeds in bogs, its range includes non-montane areas well south of Wisconsin); and (4) immigrant (tyrphoxenous)—not a year-round resident of the region and unlikely to breed in bogs. In Wisconsin, the bog specialists are all at the southern end of their eastern North American range, with their known range not extending into the state immediately south of Wisconsin, but further east *L. epixanthe* and *L. dorcas* may occur in areas more southerly than Wisconsin (Opler 1992; Glassberg 1999; Nielsen 1999).

Especially in bogs, we surveyed in a wider range of weather conditions than prescribed in Pollard (1977) and Wikström et al. (2009). We experienced severe constraints

Table 2 Total individuals of each specialist and affiliate species in bogs, lowland roadsides, and upland roadsides during 1987–2009 on formal surveys (informal observations in lowland and upland roadsides in parentheses)

Species			Bog	Lowl	Upl	Notes
Bog specialists						
L	MCK	Bog copper *Lycaena epixanthe*	3,986	674	2	23 Jun–15 Aug
N	MCK	Bog fritillary *Boloria eunomia*	1,084	0	1(1)	9 Jun–14 Jul
N	MCK	Jutta arctic *Oeneis jutta*	962	1	0	12 May–10 Jul
N	MCK	Freija fritillary *Boloria freija*	722	0	0	7 May–15 Jun
N	M	Frigga fritillary *Boloria frigga*	264	0(1)	0	19 May–20 Jun
N	M	Purplish fritillary *Boloria montinus*	192	1,093	0	27 Jul–23 Aug
L	MC	Dorcas copper *Lycaena dorcas*	163	379	0	26 Jun–15 Aug
N	M	Red-disked alpine *Erebia discoidalis*	128	1	0	10 May–14 Jun
Bog affiliates						
L		Brown elfin *Callophrys augustinus*	4,304	6	0	
N		Inornate ringlet *Coenonympha tullia*	607	167	10	
Pi		Pink-edged sulphur *Colias interior*	302	229	12	
N		Eyed brown *Satyrodes eurydice*	245	251	81	
H		Dreamy duskywing *Erynnis icelus*	168	7	2	
N		Silver-bordered fritillary *Boloria selene*	123	95	19	
N		Atlantis fritillary *Speyeria atlantis*	46	299	134	
N		Harris' checkerspot *Chlosyne harrisii*	32	29	0	
N		Green comma *Polygonia faunus*	1	0	0	

Family is abbreviated as *P* Papilionidae, *Pi* Pieridae, *L* Lycaenidae, *N* Nymphalidae, *H* Hesperiidae. Abbreviations for site types each specialist was recorded in: *M* muskeg, *C* coastal peatland, *K* kettlehole. Butterfly names follow Cassie et al. (2001)

on obtaining suitable weather especially in spring. The bog-specialist species varied greatly in detectability relative to weather. For example, temperatures of 13–14°C (if sunny) were excellent for surveying *Boloria freija*, which is active but not too active then, while *Erebia discoidalis* is most effectively surveyed at mid-day in the warmest sunniest conditions possible (at least 16°C but preferably 18–19°C or warmer as described in Swengel 2009). Both these species have similar spring flight periods (Table 2). The tan and brown color of the vegetation in spring results in warmer microclimates in and between peat hummocks relative to overall air temperature, which may facilitate butterfly activity in cooler conditions than usually recommended for butterfly surveying. The negative effect of subpar weather on butterfly detection in our survey results is not a systematic bias, as we did not (and could not) bias which sites were surveyed in better weather, so that this factor confounds statistical power, but doesn't systematically misdirect it.

Analyses

As in Nekola and Kraft (2002), we identified the flight period per species by the first and last date per year we detected it, separately for the two study regions, and in northern Wisconsin, separately for coastal peatlands, which were much later in phenology than the other sites (Swengel 2009). We also determined flight period spans separately for different areas of inland northern Wisconsin when phenological differences were evident for a particular species (e.g., *L. epixanthe* in Swengel 2009). In the case of single outlier individuals observed, we did not consider it flight period at sites where not seen. Our population index is the peak survey count per site per brood, standardized to survey time, to create an observation rate (relative abundance) per hour per unit survey. Since *Oeneis jutta* may have a two-year life cycle, with one cohort larger than the other (Opler and Krizek 1984), we tested for a skewed distribution by even and odd years. Although significantly different (Table 3), even-year cohorts were 73% the abundance of odd-year cohorts, well within the range of typical variation from annual fluctuation reported for specialist butterflies (Pollard and Yates 1993; Swengel and Swengel 2007). For this reason, we pooled all available years for this species' analyses.

Analysis was done with ABstat 7.20 software (1994 Anderson-Bell Corp., Parker, Colorado). Statistical significance was set at two-tailed $P < 0.05$. Since significant results occurred at a frequency well above that expected due to spurious Type I statistical error, the critical P value was not lowered further, as more Type II errors (biologically meaningful patterns lacking statistical significance)

Table 3 Distribution of *Oeneis jutta* individuals on peak count per year at sites ever reporting the species, by even and odd years during 2002–2009, significantly skewed from expected based on survey effort (h) in each group of years (chi square goodness of fit test $P = 0.0000$)

	Observed individuals	Survey time	Expected individuals	Observation rate (h)
Odd years	503	47.19 (54.6%)	442	10.7
Even years	307	39.26 (45.4%)	368	7.8
Total	810	86.45	810	

would be created than Type I errors eliminated. All correlations were done with the Spearman rank correlation. To test for significant skewing compared to distribution proportional to survey effort (h), we used the Chi Square Goodness of Fit test, and to test for significant differences in relative abundance among sites, we used the Mann-Whitney *U* test. All statistical tests in this study are non-parametric, which do not require any assumptions about how the data are distributed (e.g., normality).

Results

We recorded the same specialists in muskegs as in Nekola's (1998) study (Table 2). The few additional species we recorded in kettleholes and coastal peatlands within Nekola's (1998) study region were infrequently encountered in only one or two sites per bog type (in coastal peatlands, one *B. freija* at one site, five *O. jutta* at one site, and seven *L. dorcas* at two sites; in kettleholes, three *B. freija* at one site).

In analysis of the peak surveys per year of the four most frequently recorded specialists (Figs. 1, 2; Appendix 1), significant differences in abundances occurred among bog types. Significantly highest abundances of *L. epixanthe* and *B. eunomia* were in kettleholes and coastal peatlands,

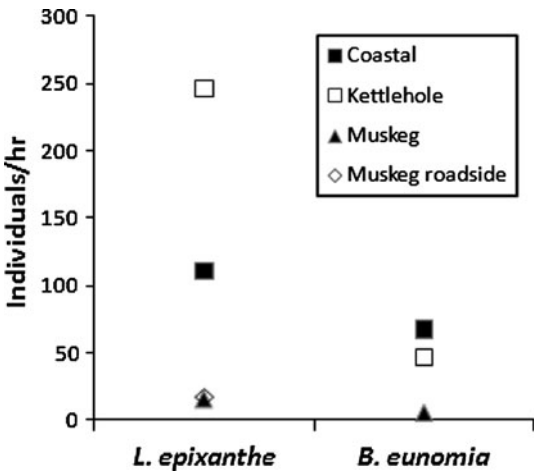

Fig. 1 Grand means of average relative abundance (peak individuals/hr per site per year) of *L. epixanthe* and *B. eunomia* in sets of sites grouped by bog type, as in "Appendix 1"

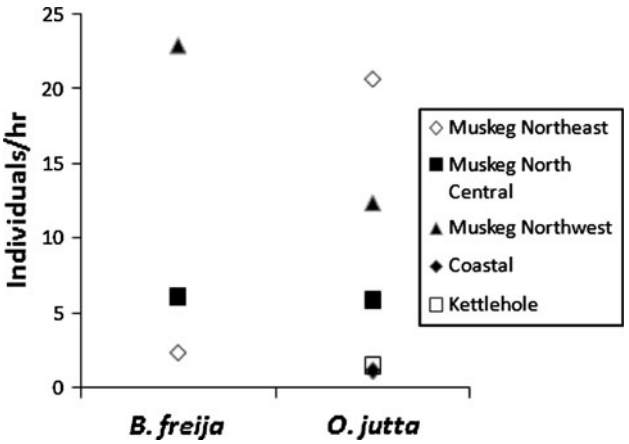

Fig. 2 Grand means of average relative abundance (peak individuals/hr per site per year) of *B. freija* and *O. jutta* in sets of sites grouped by bog type, and for muskeg, by subregion, as in "Appendix 1" (coastal peatlands and kettleholes were not plotted for *B. freija*, since we so rarely recorded it there)

despite their small size. Within each bog type, abundance of some species also significantly differed among sites (Appendix 1); for muskegs (for which we have the largest sample of sites over the greatest geographical spread), these differences occurred both within and among subregions. The percentage of years we found the species covaried significantly with mean relative abundance for each species (Table 4). Nonetheless, at muskegs with longer survey routes (Armstrong, Glidden), we had a fairly reliable detection of presence each year (50–100% of years surveyed) for species occurring in low abundance (*B. freija* at both sites, *B. eunomia* at Glidden) (Appendix 1), despite few visits (1–3) during the flight period per year.

Specialists with adequate formal sampling in nearby upland roadsides were significantly under-represented there (Fig. 3; Appendix 2). Flight period timing explained

Table 4 Coefficients (*r*) and significance (*P*) of Spearman rank correlations of proportion of years recorded as present in *N* sites to mean abundance in each site as in "Appendix 1", by species

	N	*r*	*P*
Lycaena epixanthe	27	+0.760	<0.01
Boloria eunomia	18	+0.536	<0.05
Boloria freija	15	+0.849	<0.01
Oeneis jutta	23	+0.633	<0.01

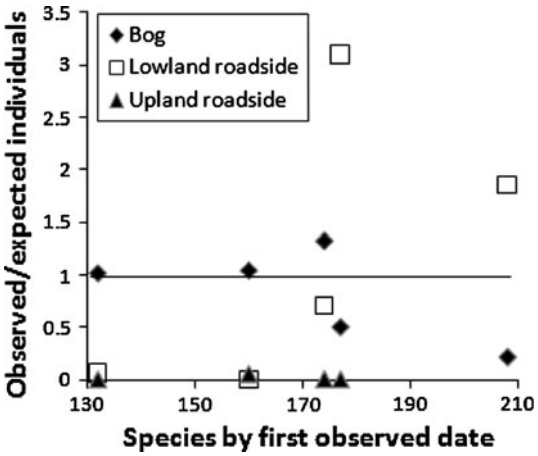

Fig. 3 Ratio of observed/expected individuals based on survey effort in bog, adjacent lowland roadside, and nearby upland roadside, by species (see "Appendix 2"), in order of first observed date (as in Table 2) expressed as sequentially numbered date. Random distribution = 1 (observed = expected)

whether bog specialists occurred in any numbers in adjacent lowland roadsides (Fig. 3; Appendix 2). Spring species were significantly under-represented there. Two summer species were significantly over-represented in these lowland roadsides compared to bogs, and the third (*L. epixanthe*) occurred in substantial numbers (Appendix 2), although still under-represented there. Bogs were relatively nectar-rich in spring, more so than the roadsides, but nectar-poor in summer, when the roadsides were nectar-rich.

L. epixanthe was remarkably detectable in cool, cloudy weather in coastal peatlands as well as inland kettleholes in the same county (Table 5). This was especially noticeable in the coastal peatlands due to the lower mean temperature and percent sunshine on surveys there. Some surveys in cool, cloudy weather produced "good" counts (Table 6), defined as abundances at least half the mean relative abundance of that site in "Appendix 1". This contrasted with inland surveys in Douglas County muskegs and adjacent lowland roadsides, which had the one significant weather effect (positive with percent sunshine) and no "good" counts in poor weather (Tables 5, 6). However, in 2009 in central Wisconsin (the hottest climate in this study), it was in poor weather that we obtained our highest count ever (82 individuals) of *L. epixanthe* there (Table 6).

Table 6 Surveys with low temperature <24°C and ≤30% sunshine with *Lycaena epixanthe* observation rate half or more the mean observation rate on peak surveys in "Appendix 1", at sites (grouped by type, subregion, and county) analyzed in the table

Site	Date	Temperature	% Sunshine	Obs rate
Coastal peatlands (Northwest: Bayfield coastal)				
Bark Bay	27 Jul 93	17	0%	64.9
Bark Bay	24 Jul 08	19	5	112.3
Bibon Lake	24 Jul 08	22	2	96.9
Port Wing Boreal Forest	24 Jul 08	19	30	228.0
Bibon Lake	23 Jul 09	17	15	114.3
Bark Bay	7 Aug 09	22	20	109.4
Kettleholes (Northwest: Bayfield interior)				
East Roger Lake	9 Jul 06	20	1	240.0
Pine Lake	24 Jul 08	22	0	525.0
East Wishbone Lake	24 Jul 09	23	25	369.2
East Wishbone Lake	9 Aug 09	21	10	200.0
Muskeg (Central: Jackson)				
Highway 54	4 Jul 09	20	0	213.9

Table 5 Spearman rank correlation coefficients (*r*) (boldfaced if significant) of peak *Lycaena epixanthe* observation rates as analyzed in "Appendix 1" with low temperature and percent sunshine on each unit survey, excluding sites (Lost Creek, East Crane Lake) significantly lower in abundance within that group of sites (see "Appendix 1")

Bog site type	Coastal	Kettlehole	Muskeg	Muskeg lowland rdside
County	Bayfield	Bayfield	Douglas	Douglas
N unit surveys	24	24	45	41
Mean temperature (°C)	18.6	24.6	25.6	25.3
Range of temperature (°C)	17–32	19–31	17–32	18–32
Mean % sunshine (%)	38.9	71.7	69.0	72.4
Range of % sunshine (%)	0–100	0–100	0–100	0–100
Correlation (*r*) with				
Low temperature	−0.224	−0.047	+0.129	−0.020
Percent sunshine	+0.255	−0.363	**+0.359**	+0.282

Discussion

Cautions

Frequent surveys under strict weather and timing protocols (e.g., Pollard 1977; Pollard and Yates 1993; Wikström et al. 2009) produce more robust results than our less frequent surveys in more variable weather and times of day. As a result, our abundance indices are more confounded by phenology and variation in detection due to weather. Therefore, the strongest findings in this study are relatively high abundances (despite these confounding factors), previously unreported presence of species in coastal peatlands and kettleholes, and results that are most consistent with others' independent findings, as discussed below.

Characterization of bog butterfly fauna

Nekola's (1998) report of *L. epixanthe* and *B. eunomia* as the dominant species in kettleholes, and the latter dominant in coastal peatlands, is consistent with the high abundances we recorded for both species in both bog types (Fig. 1) despite small bog sizes (Appendix 1). Agreeing with Nekola's (1998) report of significantly different peatland butterfly faunas among the three bog types, we found some significant differences in species' abundances among bog types (Appendix 1). Furthermore, we found significant differences in relative abundance within type among sites. Extraordinarily high abundances of a few species (*L. epixanthe*, *B. eunomia*) occurred in small kettleholes, consistent with a few reports of high numbers for *L. epixanthe* in the 4th of July butterfly counts (Opler and Powell 1984: 2000 individuals at Union City, Pennsylvania; Wander 2009: 1509 individuals at Central Franklin County, Massachusetts). High densities of *B. aquilonaris* have also been reported in European bogs (Baguette and Schtickzelle 2006). Furthermore, at two bogs of the same vegetative classification with similar host plant abundance, *B. aquilonaris* abundance varied six-fold in relation to sphagnum structure (carpet or hummock), which affected larval microclimate (Turlure et al. 2010). Small prairies can also have very high specialist numbers, e.g., 906 regal fritillaries (*Speyeria idalia*) in 1.25 h of surveying at an occasionally hayed 12 ha prairie on the Northern Loess Hills, Iowa count (Swengel and Opler 1996). Viable populations of localized butterfly have been reported for small British sites (Thomas 1984).

As Nekola (1998) noted, the North American literature indicated bog butterflies' preference for peatland margins, but that was generally not the case in his experience or ours. He noted an exception that *B. montinus* adults were primarily found at adjacent upland nectar, a description that includes flowers in the gravel edge of roads by lowland ditches adjacent to bogs. We found a few summer species, including that one, frequenting adjacent lowland roadsides but virtually none occurring in nearby upland roadsides (Fig. 3; Appendix 2). Furthermore, the use of adjacent lowland roadsides should be interpreted with caution. We sampled relatively few sites and they were biased toward opener, less brushy ditches with more of a wetland characteristic, which may exaggerate specialist use of roadsides. Some bogs, including small kettleholes and coastal peatlands, are entirely surrounded by formidable barriers (dense forest, Lake Superior). But others have places where they border more open vegetations, such as roadsides, grasslands, and marshes, so that it is not an obvious barrier (water, forest) that prevents specialist movement out of these bogs.

Movement vs. dispersal limitations

Nekola and Kraft (2002) reported significant clustering of both bog butterfly presences and absences. This may be attributable to metapopulation dynamics (both dispersal and dispersal limits). Although virtually undetected in this study (Table 2; Fig. 3; Appendix 2), some movement of specialists out of bogs and between them is still possible. As mapped in Nekola and Kraft (2002), many bogs occur in clusters with at least one other bog within 5 km. This is within or near the maximum dispersal distance reported by Baguette and Schtickzelle (2006) for two bog specialists (13.5 km for *B. aquilonaris* and 4.6 km for *B. eunomia*) and within the effective colonization distance documented for other localized butterflies (e.g., Davies et al. 2005). However, in more fragmented landscapes, bog butterflies may be particularly disinclined to disperse out of a patch (Vandewoestijne and Baguette 2004, Schtickzelle et al. 2006), with maximum dispersal usually <2 km (Mennechez et al. 2003). Many species of butterflies show variability in dispersal behavior among populations (Stevens et al. 2010), so that mobility observed in one context may not apply to another. Furthermore, examples of each bog type are mapped as >10–15 km from the next nearest bog; e.g., Pine Lake (Appendix 1) is >15 km from the next nearest bog, except for a few tiny patches much smaller than Pine Lake that we found. Thus, other factors besides metapopulation dispersal may contribute to this spatial patterning, such as subtle habitat quality factors and subdetectable numbers, leading to false negatives (a species may not be found every year in lower density sites; cf. Table 4; Appendix 1). Spatially correlated patterns today could also result from non-dispersal and non-colonization following extirpation from local catastrophes (e.g., wildfire, protracted flood, extreme drought) that may have occurred a very long time ago. It would, however, be difficult to distinguish outlier colonization events from outlier retention events.

Over geologic time, these bog-specialist butterflies had to move around the landscape because the bog vegetation they occupy now developed on topography under an ice sheet in the last glaciation (Curtis 1959, Wright 1983). By contrast, limits on their movement now are prominently apparent. Many bog specialists do not even frequent adjacent lowland roadside ditches, while all specialists seem to penetrate virtually no further than that (Tables 2; Fig. 3; Appendix 2). Bogs are scattered widely around northern Wisconsin but are <1% of the landscape as a whole (Hoffman 2002), approximately as isolated as habitat patches in highly fragmented anthropogenic landscapes, such as tallgrass prairie (Samson and Knopf 1994). Layberry et al. (1998) report additional evidence for post-glacial dispersal barriers. Tundra-adapted butterflies surviving the last Ice Age in the "Beringian Refugium" (Northern Yukon and areas westward) "dispersed northward and eastward with varying degrees of success": 32 tundra species in northern Yukon, only 11 as far east as northern Quebec. At the end of the last Ice Age, the vegetations occupied by these study species were likely not as disjunct then as they are now, given that most of these bog butterflies occupy a wider array of vegetation types in Canada now (Layberry et al. 1998). The exception is *L. epixanthe*, rather consistently restricted to bogs throughout its relatively more limited and more southerly range. More dispersal tendency may not have occurred then than now. Rather these butterflies may have occurred in more vegetation types in more of the landscape then, subsequently becoming more restricted to bogs, "high and dry" (or perhaps more appropriately, "sunk and dunked") as this vegetation became isolated patches.

Habitat quality vs. landscape configuration

Some kettleholes and coastal peatlands were relatively small and isolated (see map in Nekola and Kraft 2002) yet supported remarkably high densities of *L. epixanthe* and *B. eunomia*, as well as low but predictable numbers of *O. jutta* (Figs. 1, 2; Appendix 1), and occasionally even *B. freija* (Table 2). High habitat quality in the species-specific sense of consistently available required resources (as construed in Dennis and Eales 1997; Thomas et al. 2001; Dennis et al. 2007; Dennis 2010) appears more effective at explaining this than spatial reinforcement either from patch size or from the surrounding landscape. These dense populations of *L. epixanthe* and *B. eunomia* probably represent long-term population persistence in situ with little chance for immigration. However, some species occured only (e.g., *E. discoidalis*) or primarily (*B. freija*) in muskegs (Table 2; see "Results"), which were often larger (Appendix 1) and more connected in complexes (per map in Nekola and Kraft 2002), suggesting the value of large and connected habitat patches. Densities of some species were relatively high in some muskegs: e.g., *B. freija* (Fig. 2; Appendix 1), and cf. high numbers of *B. montinus* in the few bogs and adjacent lowland roadsides (Table 2; Fig. 3; Appendix 2) in the one county where found at all. However, while widely findable, bog specialists sometimes occurred only in small numbers: e.g., numerous sites with mean observation rates < 5/h in "Appendix 1", and these were the four most frequently recorded specialists (cf. Table 2). Pristine as these bogs are (a kind of high quality), the habitat can't be called all that good quality for those small populations–otherwise, they should be more abundant. Large size may be necessary to amass an adequate amount of required resources to sustain these populations (cf. Turlure et al. 2009, 2010), suggesting that habitat quality may be more important than it first seems in explaining the better occurrence of some specialists in bigger bogs.

Co-evolution vs. stasis

As Elias (1994) summarized, insects don't evolve out of trouble from climatic cycles; they move out of trouble. That is, remarkable stasis (species stability) is evident over millennia in the insect fossil record, but the location of these species has moved tremendously in association with vegetative changes responding to climatic oscillations (Ashworth 2001; Whitehouse 2006; Whitehouse et al. 2008). Given the low dispersal apparent today for species restricted to bogs (Spitzer et al. 1999; Spitzer and Danks 2006; see "Results"), "move" might be better understood as "hunkering" within their vegetation as it expands and shrinks and moves around the landscape. While evolution is often portrayed as an either-or choice ("adapt or die"—discussed further below), it's actually a three-way possibility: "adapt or hold out or die". On the one hand, bog butterflies evidence ongoing evolutionary change. The "*B. titania*" species complex has a European taxon and in North America, a tundra taxon and a boreal taxon (*B. montinus*, the taxon studied here); many species or species complexes have tundra (sub)species and boreal (sub)species (Layberry et al. 1998). Local races or subspecies are evident among isolated bog regions for many bog insects (Wright 1983; Spitzer and Danks 2006). On the other hand, temperate bog butterflies appear not to have co-evolved at all; they're hunkering in with the way of living they've been doing with remarkable long-term faunal stability, even though they can do this only in a very small part of the landscape (<1%) in Wisconsin (per Hoffman 2002).

Even what might look like evolution may not be after all. *L. epixanthe* in coastal peatlands had seemed more detectable in poorer weather than in sites further inland

(such as Douglas County muskegs) (Table 5), until we encountered the high density in central Wisconsin (Table 6) immediately after a drenching thunderstorm. This could instead be explained as pre-existing behavioral plasticity expressed differently in different circumstances. Likewise, dispersal tendency may evolve in response to varying degrees of habitat fragmentation (as described in Baguette et al. 2003; Hanski and Pöyry 2007) or the same pre-existing behavioral repertoire may instead be expressed differently depending on varying landscape circumstances as well as individual variation.

Some European butterflies have an affinity (even apparent modern-day restriction) to some forms of old-fashioned, unintensive agriculture and forest harvesting (van Swaay and Warren 2006). Although this apparent dependence may be attributed at least in part to co-evolution, this is often explained as butterflies expanding or contracting in these semi-natural landscapes based on the species' predispositions for these resources and conditions, without necessarily co-evolving (Erhardt and Thomas 1991; Dennis 1992; Dennis 2010). This latter is more consistent with the apparent lack of ongoing co-evolution occurring in the modern landscape (why would it stop a century or two ago?), and with the present-day "biodiversity crisis" most marked for more specialized species, but even affecting numerous widely occurring species (Maes and Van Dyck 2001; van Swaay et al. 2006; Dennis 2010).

Many assert co-evolution of prairie biota with fire (e.g., Curtis 1959; Wisconsin DNR 1995; Packard and Mutel 1997). Apart from controversy over just how much fire actually occurred prehistorically (cf. Higgins 1986; Umbanhowar 1996; Russell 1997), this assumes aboriginal inhabitants as a single culture applied fire in an inescapable and frequent way everywhere to become an unequivocal and unavoidable evolutionary pressure (forcing the outcome down to "adapt or die"). Even modern civilization hasn't fully and uniformly transformed the entire landscape, witness the continued existence of never-plowed botanically "high quality" prairie as well as temperate-zone bogs in very small proportions of the landscape (see "Introduction"). If instead Native Americans varied among clans and tribes in activity and culture, with variable influence on the landscape (Russell 1997), including no-man's zones between antagonistic tribes as reported in Martin and Szuter (1999), then butterflies could sort themselves out along such gradients as fire frequency and native herbivory pressure mediated by variable aboriginal hunting pressure. Some butterflies may have co-evolved in some form, but others may have successfully hunkered in, possibly in very small parts of the landscape, just as bog butterflies have reliably persisted in the <1% of Wisconsin that is bog.

Whether it's co-evolution or not is less important when management proceeds based on conservation evidence for the species affected, as promulgated in Pullin and Knight (2001). But when conservation implements ecosystem management based on theoretical assumptions instead, then picking the right theory (e.g., co-evolution or stasis) becomes critical.

Conclusions for conservation

Dispersal, colonization, and landscape configuration matter (Dennis and Eales 1997; Thomas et al. 2001; Hanski and Pöyry 2007; Dover and Settele 2009; Dennis 2010). If metapopulation dynamics and/or the ecosystem approach are successfully conserving a particular site's insects (e.g., Davies et al. 2005), continue that. If not (e.g., specialist declines in relatively large preserves as in Schlicht et al. 2009), then it may be appropriate to imitate how nature maintains regionally appropriate numbers of highly localized bog butterflies in extremely fragmented patches via remarkable vegetative stability, as well as high habitat quality in the species-specific sense on small sites. Instead of relying on colonization, focus instead on retention because the otherwise inevitable long-term outcome for rare species is to have many more extirpations than colonizations (Bulman et al. 2007). This approach can be applied via detailed species-specific knowledge, but where that is lacking, the following multi-species/ecosystem approaches are indicated (in addition to vigorous effort to acquire species-specific knowledge). Be retrospective (not prospective) in continuing site stability (maintain consistency with past site management before investigating subtle, gradual approaches to restoration). Do not conflate vegetative variation among locations with change within a location (vegetative heterogeneity can be compatible with location-specific consistency).

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Appendix 1

See Table 7.

Table 7 Mean relative abundance (individuals/h) of four most abundant specialists on unit surveys of peak survey per site per year during 2002–2009, by groups of sites, sorted by bog type (with subregion and counties in parentheses)

	Years	Mean	SD	Size	Significance within among
Lycaena epixanthe					
Kettleholes (Northwest: Bayfield interior)					A
East Crane Lake	4/4	23.7	8.1	7.82	B
East Roger Lake	7/7	222.3	194.9	1.84	A
East Wishbone Lake	7/7	335.5	181.2	4.12	A
Pine Lake	4/4	404.8	374.9	1.96	AB
Coastal Peatlands (Northwest: Bayfield coastal)					B
Bark Bay	8/8	101.1	61.9	9.23	A
Bibon Lake	7/7	109.9	65.0	16.56	A
Lost Creek	6/6	28.5	19.7	2.93	B
Port Wing Boreal Forest	4/4	204.3	142.6	2.40	A
Muskegs (Northwest: Douglas)					C
Bear Lake	6/7	17.5	11.8	72.02[a]	A
Bear Lake North	4/6	12.4	21.7	72.02[a]	AB
Lyman Lake	7/8	9.8	17.4	50.55	B
Milchesky Road	7/8	29.5	37.3	114.80	AB
Muskeg lowland roadsides (Northwest: Douglas)					C
Bear Lake	8/8	35.3	50.6		A
Bear Lake North	6/8	32.9	59.4		A
Lyman Lake	3/8	4.1	6.0		A
Milchesky Road	3/8	45.9	93.5		A
Muskegs (North Central: Ashland, Iron, Price)					C
Caroline Lake	5/5	28.7	29.7	52.58	A
Glidden	8/8	20.0	31.8	80.16	A
Highway 70/137	3/4	5.8	5.3		A
Muskeg lowland roadsides (North Central: Ashland, Iron)					C
Caroline Lake	1/4	2.7	5.5		A
Caroline Lake east 0.2	0/3	0.0	0.0		–
Caroline Lake east 1.0	0/3	0.0	0.0		–
Glidden	6/8	20.7	31.8		A
Muskegs (Northeast: Forest)					C
Armstrong	8/8	20.1	31.8		A
Forest Road 2182 West	4/6	14.2	16.7		A
Forest Road 2182/2414	4/7	5.0	6.3		A
Forest Road 2414	4/7	4.6	5.7		A
Boloria eunomia					
Kettleholes (Northwest: Bayfield interior)					A
East Crane Lake	4/6	36.7	57.6	7.82	A
East Roger Lake	6/6	85.5	66.1	1.84	A
East Wishbone Lake	6/6	48.4	56.6	4.12	A
Pine Lake	5/6	22.6	16.5	1.96	A
Coastal Peatlands (Northwest: Bayfield coastal)					A
Bark Bay	7/7	43.0	39.5	9.23	BC
Bibon Lake	7/7	59.6	39.8	16.56	AB
Lost Creek	6/7	24.0	17.4	2.93	C
Port Wing Boreal Forest	7/7	144.0	124.5	2.40	A

Table 7 continued

	Years	Mean	SD	Size	Significance within among
Muskegs (Northwest: Douglas)					B
Bear Lake	7/7	5.2	6.4	72.02[a]	A
Bear Lake North	6/7	8.2	9.3	72.02[a]	A
Lyman Lake	5/8	2.8	4.4	50.55	A
Milchesky Road	5/7	4.6	5.0	114.80	A
Muskegs (North Central: Ashland, Price, Washburn)					B
Glidden	8/8	1.8	4.8	80.16	C
Highway 77	5/6	5.9	4.7		AB
Forest Road 137 1.9	2/5	1.2	2.9		C
Forest Road 137 2.3	2/5	2.3	3.3		BC
Highway 70/137	4/4	15.8	8.9		A
Muskegs (Northeast: Forest)					B
Armstrong	6/6	5.7	10.8	–	
Boloria freija					
Muskegs (Northwest: Douglas)					A
Bear Lake	8/8	31.0	14.7	72.02[a]	A
Bear Lake North	7/7	25.9	15.3	72.02[a]	A
Lyman Lake	8/8	17.8	17.5	50.55	A
Milchesky Road	8/8	16.7	13.6	114.80	A
Muskegs (North Central: Ashland, Iron, Price)					B
Caroline Lake	5/5	16.5	13.3	52.58	A
Glidden	4/7	0.9	2.6	80.16	CD
Forest Road 137 1.2	4/8	2.8	5.0		C
Forest Road 137 1.9	7/8	6.4	7.6		AB
Forest Road 137 2.3	6/8	6.2	9.8		AB
Forest Road 505 1.6	7/7	4.0	6.4		BC
Muskegs (Northeast: Forest)					C
Forest Road 2182 0.5	7/8	8.4	7.0		A
Forest Road 2182 1.4	1/8	1.0	2.9		B
Forest Road 2182/2414	2/7	0.9	1.6		B
Forest Road 2414	2/8	0.8	1.5		B
Armstrong	4/8	0.6	2.5		B
Oeneis jutta					
Kettleholes (Northwest: Bayfield interior)					CD
East Roger Lake	1/5	0.7	1.6	1.84	AB
East Wishbone Lake	1/6	0.6	1.5	4.12	B
East Crane Lake	4/5	4.6	4.4	7.82	A
Pine Lake	0/4	0.0	0.0	1.96	AB
Coastal Peatlands (Northwest: Bayfield coastal)					D
Bark Bay	0/6	0.0	0.0	9.23	B
Bibon Lake	5/7	3.6	2.6	2.40	A
Lost Creek	0/5	0.0	0.0	2.93	AB
Port Wing Boreal Forest	0/6	0.0	0.0	16.56	B
Muskegs (Northwest: Douglas)					B
Bear Lake	8/8	11.2	15.5	72.02[a]	AB
Bear Lake North	8/8	19.3	12.8	72.02[a]	A
Lyman Lake	8/8	11.3	12.2	50.55	B
Milchesky Road	5/7	7.9	6.9	114.80	B

Table 7 continued

	Years	Mean	SD	Size	Significance within among
Muskegs (North Central: Ashland, Iron, Price, Washburn)					AC
Glidden	7/8	6.0	10.9	80.16	A
Highway 77	5/7	7.4	6.4		A
Forest Road 137 1.9	6/8	10.1	15.9		A
Forest Road 137 2.3	6/7	4.6	7.3		A
Highway 70/137	1/4	1.2	2.4		A
Caroline Lake	4/5	6.0	6.0	52.58	A
Muskegs (Northeast: Forest)					A
Forest Road 2182 0.5	4/8	14.4	18.5		AB
Forest Road 2182 1.4	5/7	32.3	31.7		A
Armstrong	6/7	10.2	22.7		B
Forest Road 2182/2414	5/7	17.9	16.0		AB
Forest Road 2414	5/7	28.5	31.3		AB

"Yrs" = *N* years found/*N* years surveyed. Patch size (ha) provided by J. Nekola (personal communication), except we estimated patch size for Port Wing Boreal Forest. For each species, within each group of sites, sites sharing no letters are significantly different, and among groups, groups sharing no letters are significantly different: A, significantly highest; B, significantly lower than A; C, significantly lower than B, and so on

[a] Treated as one site by J. Nekola (personal communication)

Appendix 2

See Table 8.

Table 8 Distribution of specialist individuals in bog, adjacent lowland roadsides, and nearby upland roadsides during the entire study, in order of first observed date in Table 2

	Bog	Lowland roadside	Upland roadside
B. freija			
Observed	722	0	0
Survey time	100.0		
E. discoidalis			
Observed	128	1	0
Survey time	71.7		
Oeneis jutta			
Observed	962 **(99.9%)**	1 (0.1%)	0 (0.0%)
Expected	940.9 (97.7%)	14.9 (1.6%)	7.1 (0.7%)
Survey time	159.6	2.5	1.2
B. frigga			
Observed	264	0 (1)	0
Survey time	107.9		
B. eunomia			
Observed	1084 **(99.9%)**	0 (0.0%)	1 (1) (0.1%)
Expected	1035.3 (95.4%)	30.6 (2.8%)	19.1 (1.8%)
Survey time	82.4	2.4	1.5
L. epixanthe			
Observed	3986 **(85.5%)**	674 (14.5%)	2 (0.0%)
Expected	2995.7 (64.3%)	946.0 (20.3%)	720.2 (15.4%)
Survey time	91.7	29.0	22.0
L. dorcas			
Observed	161 (29.4%)	386 **(70.6%)**	0 (0.0%)
Expected	319.7 (58.5%)	124.5 (22.8%)	102.8 (18.8%)
Survey time	61.0	23.8	19.6
B. montinus			
Observed	192 (11.1%)	1538 **(88.9%)**	(0)
Expected	898.7 (52.0%)	831.3 (48.0%)	
Survey time	23.4	21.6	

Observed individuals for each species are significantly skewed relative to expected based on proportion of survey time (h) in each site type (chi square goodness of fit $P = 0.0000$ for each species). Most over-represented is boldfaced; most under-represented is underlined. If roadside survey time was <1 h, that site type was excluded from statistical analysis but *N* individuals observed on those surveys is provided. *N* individuals on informal observations is in parentheses but excluded from analysis

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